ZOOLOGICAL SCIENCE 8: 135–146 (1991)

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Biogeographic Patterns in Waving Display, and Body Size and Proportions of *Macrophthalmus japonicus* Species Complex (Crustacea: Brachyura: Ocypodidae)

Keiji Wada

Department of Biology, Faculty of Science, Nara Women's University, Nara 630, Japan

ABSTRACT—Two closely related ocypodid crabs, *Macrophthalmus japonicus* (De Haan) and *M. banzai* Wada & Sakai, show partly sympatric distribution, with the former species ranging more northward than the latter. Patterns of male waving display, that differ distinctively between the two species, were the same within each species among different localities. Geographic variations were described in the both species for carapace width at puberty, carapace length relative to carapace width, and propodus length of male cheliped relative to carapace width. Interspecific differences could be observed in these morphometric characters. Geographic variations of the characters within each species seemed to be related to oceanic to thalassic or exposed to sheltered situations of localities.

INTRODUCTION

Two closely related ocypodid crabs, *Macrophthalmus japonicus* (De Haan, 1835) and *M. banzai* Wada & Sakai, 1989, had been treated as one species under the name of *M. japonicus* because of their similarity in appearance until separated by Wada and Sakai [1]. Wada and Sakai [1] presented some morphological characters distinguishing the two species, together with their distinctive male waving displays. Although distributional records of these species were enumerated in Wada and Sakai [1], geographic variations in morphology and waving display were only preliminarily presented by Wada [2].

In this paper, based on the known and newly obtained data, geographic distributions of these species are summarized and the geographic trends observed in waving display, and body size and proportions are shown and discussed.

MATERIALS AND METHODS

Distributional records

Distributional records of the two species have been given by Dai and Song [3], Fukui *et al.* [4], and Wada and Sakai [1]. *Macrophthalmus japonicus frequens* and *M. japonicus japonicus* in Dai and Song [3] correspond to *M. japonicus* and *M. banzai,* respectively, and Form L of *M. japonicus* in Fukui *et al.* [4] to *M. banzai,* as revealed by Wada and Sakai [1]. The distributional records of the following specimens in author's collection should be added. *M. japonicus* **Japan**: 82♂♂54♀♀, Asadokoro, Aomori Pref., July 28, 1980/July 8, 1982, leg. K. Wada; 34♂♂39♀♀, Gamô, Miyagi Pref., July 30, 1980, leg. K. Wada; 49♂♂53♀♀, Obitsu River, Chiba Pref., May 3, 1981/Nov. 27, 1985, leg. K. Wada; 46♂♂54♀♀, Matsunase, Mie Pref., June 23, 1981/Aug. 3, 1981, leg. S. Saba; 10♂♂, Waka River, Wakayama Pref., July 1, 2, 1977, leg. K. Wada; 3♂♂2♀♀, Sumoto, Awaji-shima Is., Sept. 14, 1984, leg. K. Wada; 2♂♂1♀, Mukaishima, Hiroshima Pref., Apr. 2, 1985, leg. K. Wada; 66♂♂69♀♀, Yokonami, Kôchi Pref., June 29, 1984, leg. K. Wada; 2♂♂1♀, Mishô, Ehime Pref., July 1, 1984, leg. K. Wada; 2♂♂, Shigenobu River, Ehime Pref., July 2, 1984, leg. K. Wada; 20♂♂12♀♀, Wajiro, Fukuoka Pref., Aug. 10, 1975, leg. K. Wada; 2♂♂, Tomioka, Kumamoto Pref., Aug. 8, 1975, leg. K. Wada; 2♂♂, Makurazaki, Kagoshima Pref., July 27, 1984, leg. K.

Accepted June 7, 1990
Received March 14, 1990

Wada; 60♂♂70♀♀, Inari River, Kagoshima Pref., July 26, 1984, leg. K. Wada; 5♂♂1♀, Kôme River, Tanega-shima Is., July 31, 1984, leg. K. Wada. **Korea**: 31♂♂8♀♀, Nagdong River, Oct. 3–5, 1987, leg. S. Takeda.

M. banzai **Japan**: 30♂♂, Waka River, Wakayama Pref., June 17 & 19/July 1 & 2, 1977, leg. K. Wada; 2♂♂2♀♀, Mukaishima, Hiroshima Pref., Apr. 2, 1985, leg. K. Wada; 37♂♂50♀♀, Yokonami, Kôchi Pref., June 29, 1984, leg. K. Wada; 3♂♂1♀, Mishô, Ehime Pref., July 1, 1984, leg. K. Wada; 8♂♂, Tomioka, Kumamoto Pref., Aug. 8, 1975, leg. K. Wada; 2♂♂1♀, Makurazaki, Kagoshima Pref., July 26, 1984, leg. K. Wada; 50♂♂52♀♀, Kôme River, Tanega-shima Is., July 31, 1984, leg. K. Wada; 73♂♂27♀♀, Tatsugô, Amami-Ôshima Is., Nov. 18 & 19, 1983, leg. K. Wada; 6♂♂4♀♀, Sumiyô River, Amami-Ôshima Is., Nov. 20, 1983, leg. K. Wada; 97♂♂96♀♀, Ôura River, Okinawa-jima Is., Dec. 11, 1981, leg. K. Wada; 2♂♂2♀♀, Naha, Okinawa-jima Is., Dec. 8, 1981, leg. K. Wada; 88♂♂77♀♀, Shimoji, Miyako-jima Is., Dec. 20 & 21, 1984, leg. K. Wada; 1♂1♀, Nagura Bay, Ishigaki-jima Is., Oct. 21, 1982, leg. K. Wada; 69♂♂76♀♀, Urauchi River, Iriomote-jima Is., Oct. 18 & 19, 1982, leg. K. Wada. **Korea**: 15♂♂12♀♀, Shinoeri, Namyang, Sept. 24 & 25, 1987, leg. S. Takeda; 19♂♂11♀♀, Tokchok Is., Sept. 20, 1987, leg. B. L. Choe; 7♂♂3♀♀, Anmyun Is., May 29, 1987, leg. B. L. Choe; 8♂♂, Mokpo, Oct. 20, 1985, leg. B. L. Choe; 4♂♂, Nagdong River, Oct. 4 & 5, 1987, leg. S. Takeda. **China**: 2♂♂, Tsingtao, June 30, 1988, leg. H. Mukai; 1♂, Hangchow Bay, Che Kiang, July 7, 1988, leg. H. Mukai.

Waving display

Male waving display was recorded at 4 localities (Locality Nos. 1, 5–7 in Fig. 1) for *M. japonicus* and at 8 localities (Locality Nos. 5, 6, 8–12 & 16 in Fig. 1) for *M. banzai,* with an 8 mm movie camera. In recording the display ambient temperatures were also taken. The pattern of waving display differs conspicuously between the two speceis [1], i.e. *M. japonicus* keeps both chelipeds folded during the entire movement of a stroke (the folded type), whereas *M. banzai* unfolds the both chelipeds at the wave peak (the unfolded type). At each locality, the type of the waving display of each species was noted. Waving displays performed by males that had mature-shaped chelae and were not approaching a neighbor were chosen for determination of wave duration by frame analysis. Since this behavior was recorded at 18 or 24 frames per second, the duration of one wave stroke was determined by multiplying the number of frames involved by 56 or 42 msec depending on the recording speed. The mean wave duration for each local population was obtained by averaging the mean values of respective crabs.

Morphometric data

Specimens of *M. japonicus* obtained from 8 localities in Japan and Korea, and those of *M. banzai* from 10 localities in Japan, Korea and Taiwan (Fig. 1) were used for morphometric analysis. Sampling dates for these specimens are shown in the above *Distributional records* except for specimens from Shirahama, Wakayama Pref. (July 24, Aug. 24–26, Sept. 8, 1976 and July 31, 1981) and Taiwan (Nov. 3 & 18, 1988). The following were measured for each specimen: carapace length (CL), along the median line, from the anterior to the posterior margin; carapace width (CW), between the external orbital angles (not the widest part of carapace); propodus length of male cheliped (PL), from the ventral articulation with the carpus to the tip of the immovable finger. As secondary sexual characters, the presence of a large wedge-shaped tooth on the cutting edge of the immovable finger of the chela was checked for males, and the widening of the abdomen for females.

RESULTS

Geographic distribution

Geographic distributions of *Macrophthalmus japonicus* and *M. banzai* are summarized in Figure 2. *M. japonicus* has been recorded from Honshu, Shikoku, Kyushu and Tanega-shima Is. of Japan, and the continental coast of Yellow Sea and northern East China Sea, whereas *M. banzai* from southwestern Honshu, Shikoku, Kyushu and the Nansei-shotô Isls. of Japan, the continental coast

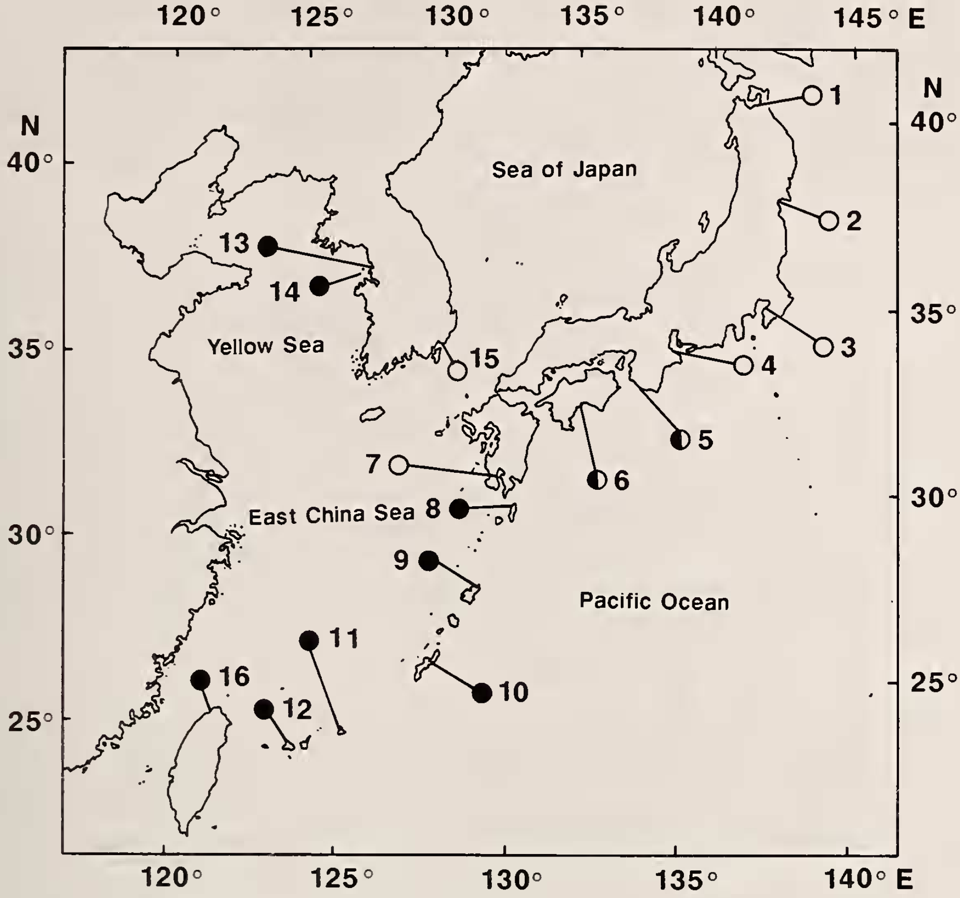

FIG. 1. A map showing localities for specimen examination and records of waving display. Open, solid and half-solid circles indicate the localities where specimens of *Macrophthalmus japonicus, M. banzai* and both species, respectively, were examined. 1: Asadokoro, Aomori Pref., 2: Gamô, Miyagi Pref., 3: Obitsu River, Chiba Pref., 4: Matsunase, Mie Pref., 5: Shirahama, Wakayama Pref., 6: Yokonami, Kôchi Pref., 7: Inari River, Kagoshima Pref., 8: Kôme River, Tanega-shima Is., 9: Tatsugô, Amami-Ôshima Is., 10: Ôura River, Okinawa-jima Is., 11: Shimoji, Miyako-jima Is., 12: Urauchi River, Iriomote-jima Is., 13: Shinoeri, Namyang, 14: Tokchok Is., 15: Nagdong River, 16: Chuwei, Tanshui.

of East China Sea and southern Yellow Sea, and Taiwan. Thus, *M. japonicus* is distributed more northward than *M. banzai* and they show partly sympatric distribution.

Waving display

Data on the waving display recorded at 10 localities are given in Table 1. *M. japonicus* showed the same folded type at all 4 localities, and *M. banzai* the same unfolded type at all 8 localities. In *M. japonicus* the mean value of wave duration ranged from 0.80 to 0.99 sec among the 4 localities and differed significantly among localities (ANOVA, $P<0.01$). The mean value of wave duration of *M. banzai* ranged from 1.25–2.22 sec among 7 localities and differed significantly among localities (ANOVA, $P<0.0005$). In particular, the mean values in the populations from Amami-Ôshima and Okinawa-jima Isls. (Locality Nos. 9 & 10) were about 1.5 times larger than those from other localities. The longer wave duration recorded for *M. banzai* in these two localities may be attributed to lower ambient temperatures during display recording (see Table 1). Even at the same

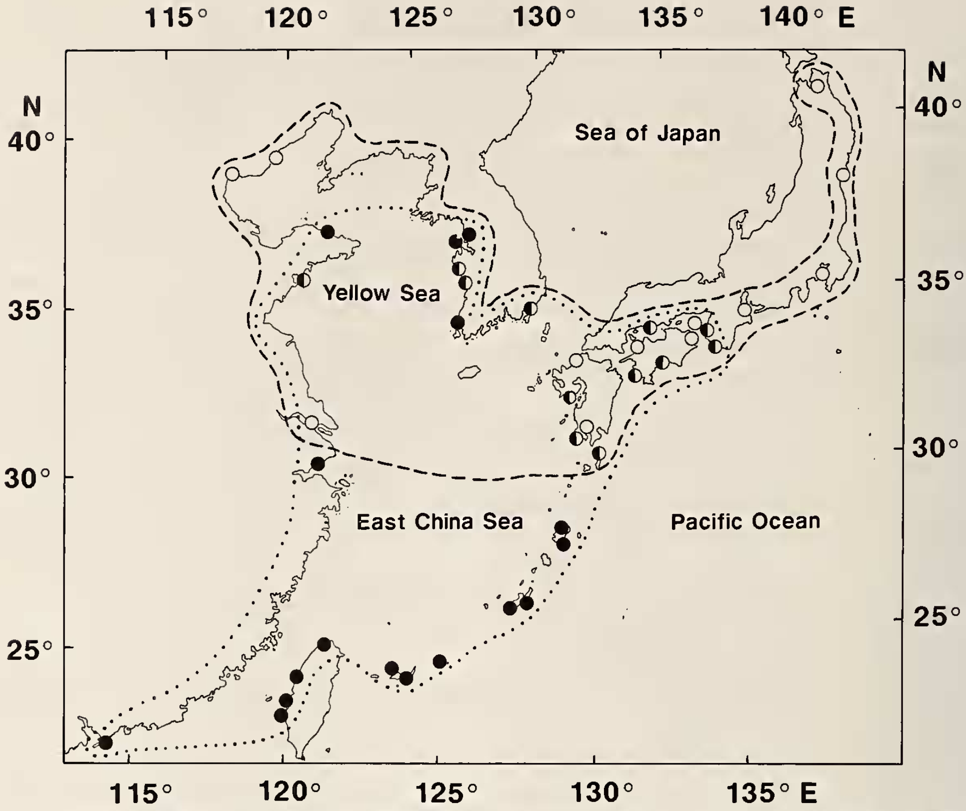

Fig. 2. Geographic distributions of *Macrophthalmus japonicus* and *M. banzai*. The localities where *M. japonicus* (open circle), *M. banzai* (solid circle) and both species (half-solid circle) have so far been recorded are shown.

Table 1. Wave type and mean wave duration (sec) in *Macrophthalmus japonicus* and *M. banzai* recorded at various localities, together with the data and air temperature. The localities (1–16) as in Fig. 1. They are arranged according to the latitude for each species. F: folded type, U: unfolded type, S.E.: standard error of the mean. For wave type, see the text

Locality	Date	Air temp. (°C)	Wave type	No. waves	No. crabs	Wave duration Mean±S.E.
M. japonicus						
1	July 6–8, 1982	20.6–26.0	F	112	25	0.97±0.04
5	Aug. 24–25, 1984	29.0–31.7	F	103	15	0.80±0.03
	June 3–5, 1985	21.5–26.0	F	113	22	0.99±0.03
6	June 28–29, 1984	25.0–27.4	F	45	7	0.82±0.04
7	July 26, 1984	28.5–31.9	F	66	13	0.92±0.04
M. banzai						
5	Aug. 24–25, 1984	29.0–31.7	U	157	46	1.25±0.04
	June 3–6, 1985	21.5–26.0	U	119	34	1.33±0.03
6	June 28–29, 1984	25.0–27.4	U	28	8	1.48±0.07
8	July 31, 1984	25.3–28.0	U	76	18	1.43±0.04
9	Nov. 19, 1983	20.7–21.0	U	67	15	2.22±0.10
10	Dec. 10–11, 1981	19.2–22.1	U	38	21	2.04±0.05
11	Dec. 20–21, 1984	20.5–24.2	U	129	41	1.39±0.03
12	Oct. 18, 1982	26.5–27.0	U	21	9	1.37±0.12
16	Nov. 1–3, 18, 1988	19.6–29.0	U	117	36	1.41±0.04

locality (Shirahama: Locality No. 5) the wave durations were significantly longer in June than in August in the both species (Duncan's multiple range test, $P<0.05$). This fact may be also caused by lower ambient temperature during display recording in June than in August (see Table 1).

Body size and proportions

For each local population of *M. japonicus* and *M. banzai,* linear regression equations between carapace width (CW) and carapace length (CL) were obtained separately for males and females (Table 2). Then, based on these equations, CL values were estimated against three CW values of 10, 15 and 25 mm (Table 3). The CL value to each CW value was larger in *M. japonicus* than in *M. banzai* excluding the two Korean populations (Locality Nos. 13 & 14). Within *M. japonicus* the population from Aomori Pref. (Locality No. 1) showed larger CL values, compared with other populations. In *M. banzai,* the CL values of the two Korean populations (Locality Nos. 13 & 14) were larger than those of other populations and similar to those of *M. japonicus*. *M. banzai* populations from Amami-Ôshima, Okinawa-jima and Miyako-jima Isls. (Locality Nos. 9–11) showed smaller CL values, compared with other conspecific populations.

The CW ranges of male crabs with the secondary sexual character and those without it are shown separately for local populations in Figure 3. The minimum CW size of the crabs with the character, which is regarded as corresponding with size at puberty, was larger in *M. japonicus* than in *M. banzai.* Within *M. japonicus* the sizes were larger in the populations from Aomori, Mie, and Kagoshima Prefs. (Locality Nos. 1, 4 & 7) than in other populations. In *M. banzai* the size of the Korean population from Sinoeri, Namyang (Locality No. 13), was larger than those of other popula-

TABLE 2. Constants for regression equations ($Y=a+bX$) (X: carapace width in mm; Y: carapace length in mm) in *Macrophthalmus japonicus* and *M. banzai* from various localities. The localities (1–16) as in Fig. 1. They are arranged according to the latitude for each species. N: sample numbers

Locality	Males					Females				
	N	Range (X)	a	b	r	N	Range (X)	a	b	r
M. japonicus										
1	82	9.50–40.00	0.678	0.664	0.999	54	9.20–38.25	0.606	0.674	0.998
2	34	12.60–28.85	0.216	0.673	0.997	39	11.30–31.90	0.384	0.664	0.996
3	49	9.05–33.45	0.513	0.662	0.998	53	10.05–29.40	0.263	0.669	0.995
15	31	11.65–27.20	0.526	0.660	0.995		No data			
4	46	5.95–27.80	0.694	0.645	0.999	54	7.50–26.10	0.645	0.643	0.997
5	66	9.95–31.10	0.483	0.661	0.997	36	8.90–28.35	0.419	0.663	0.998
6	66	8.05–30.30	0.562	0.655	0.999	69	8.45–31.30	0.505	0.662	0.999
7	60	10.70–33.55	0.532	0.656	0.998	70	11.45–32.40	0.180	0.675	0.997
M. banzai										
13	15	13.50–29.45	0.783	0.651	0.997	12	14.35–24.95	0.477	0.674	0.992
14	19	15.05–23.70	1.565	0.621	0.992	11	16.35–24.00	1.024	0.644	0.996
5	82	7.05–23.05	0.805	0.610	0.994	39	7.45–20.15	0.758	0.619	0.996
6	37	12.45–26.30	0.794	0.607	0.991	50	12.55–22.70	0.420	0.635	0.991
8	50	9.40–21.30	0.631	0.608	0.992	52	11.65–19.55	0.217	0.637	0.959
9	73	5.90–15.90	1.006	0.554	0.986	127	6.45–16.90	1.161	0.540	0.979
10	97	4.65–14.75	0.686	0.578	0.995	96	4.55–16.15	0.728	0.576	0.996
16	76	5.50–24.70	0.429	0.619	0.997	70	5.70–18.95	0.233	0.630	0.992
11	88	6.80–17.95	0.652	0.579	0.992	77	7.50–20.75	0.597	0.584	0.995
12	69	6.60–25.10	0.826	0.580	0.995	76	4.80–23.20	0.835	0.589	0.995

TABLE 3. Estimated values (in mm) of carapace length for three values (10, 15 & 25 mm) of carapace width (CW) from linear regression equations (Table 2) in each of *Macrophthalmus japonicus* and *M. banzai* from various localities. When each of 10, 15 and 25 mm is beyond the CW range of the samples from each locality, carapace length value is not given. The localities (1–16) as in Fig. 1. They are arranged according to the latitude for each species

Locality	Males			Females		
	CW=10	CW=15	CW=25	CW=10	CW=15	CW=25
M. japonicus						
1	7.32	10.63	17.27	7.35	10.72	17.47
2		10.31	17.04		10.34	16.98
3	7.13	10.44	17.06		10.30	16.99
15		10.42	17.01		9.93	17.08
4	7.14	10.38	16.83	7.08	10.29	16.73
5	7.09	10.40	17.02	7.05	10.36	16.99
6	7.11	10.39	16.93	7.13	10.44	17.06
7		10.37	16.93		10.31	17.06
M. banzai						
13		10.55	17.06		10.58	
14		10.87			10.69	
5	6.90	9.95		6.94	10.04	
6	6.86	9.90	15.97	6.77	9.94	
8	6.71	9.74		6.59	9.77	
9	6.54	9.31		6.56	9.26	
10	6.46			6.49	9.37	
16	6.62	9.71		6.53	9.68	
11	6.44	9.34		6.43	9.35	
12	6.62	9.52	15.33	6.72	9.67	

tions, and the sizes of the populations from Amami-Ôshima, Okinawa-jima and Miyako-jima Isls. (Locality Nos. 9–11) were smaller than those of other populations.

The CW ranges of female crabs with the secondary sexual character and those without it are shown separately for the local populations in Figure 4. The minimum CW size of the crabs with the character, which is considered as corresponding with size at puberty, was larger in *M. japonicus* than in *M. banzai* excluding the two Korean populations (Locality Nos. 13 & 14). Within *M. japonicus* the sizes were larger in the populations from Aomori, Chiba, Mie and Kagoshima Prefs. (Locality Nos. 1, 3, 4 & 7) than from Miyagi, Wakayama and Kôchi Prefs. (Locality Nos. 2, 5 & 6). In *M. bazai* the size of the Korean population from Sinoeri, Namyang (Locality No. 13), was larger than those of other populations and similar to those of *M. japonicus*. The females of *M. banzai* from Amami-Ôshima, Okinawa-jima and Miyako-jima Isls. (Locality Nos. 9–11) showed the character at smaller body sizes than those from other localities.

Although the length of male chela relative to CW in brachyuran crabs is closely approximated to the allometric equation, the relationship is generally different between pre-puberty and post-puberty [5]. For fully-matured males of each local population of *M. japonicus* and *M. banzai*, regression equations between CW and PL were obtained (Table 4), and depicted in Figure 5. As fully-matured males, crabs larger than the maximum size of crabs without the secondary sexual character were taken for each population. The sample of *M. banzai* from Tokchok Is. (Locality No. 14) was

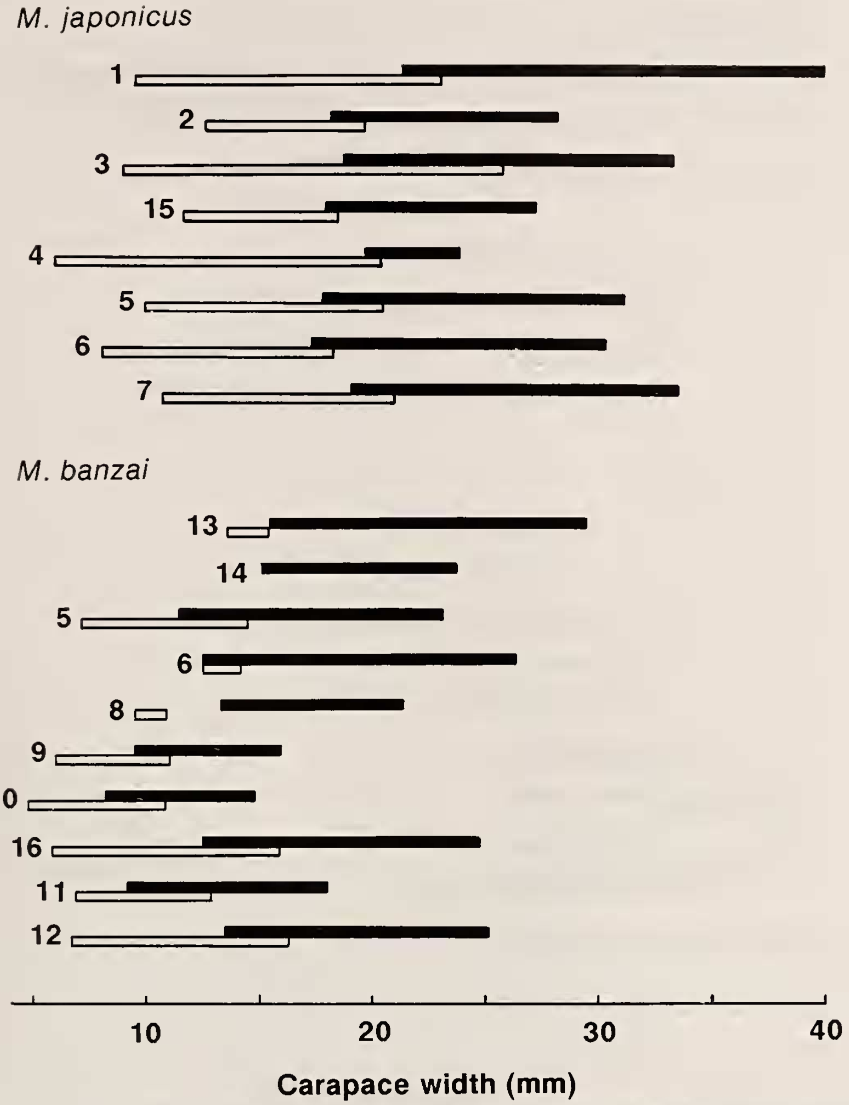

FIG. 3. Ranges of carapace widths of male crabs possessing a large tooth on the cutting edge of the immovable fingers (solid bar), and of those lacking it (open bar), in *Macrophthalmus japonicus* and *M. banzai* from various localities. Numerals by respective bars refer to the localities as in Fig. 1. The localities are arranged according to the latitude for each species.

composed only of crabs with the secondary sexual character, and all the specimens were used for the obtaining of the regression equation. Evidently, PL relative to CW was smaller in *M. japonicus* than in *M. banzai* excluding the two Korean populations (Locality Nos. 13 & 14). In *M. banzai* PL relative to CW of the two Korean populations (Locality Nos. 13 & 14) was smaller than those of other populations, being almost the same as in *M. japonicus*. *M. banzai* populations from Amami-Ôshima, Okinawa-jima and Miyako-jima Isls. (Locality Nos. 9–11), on the contrary, showed larger PL relative to CW than other conspecific populations. Within *M. japonicus* PL relative to CW of the populations from Aomori, Chiba, Mie and Kagoshima Prefs. (Locality Nos. 1, 3, 4 & 7),

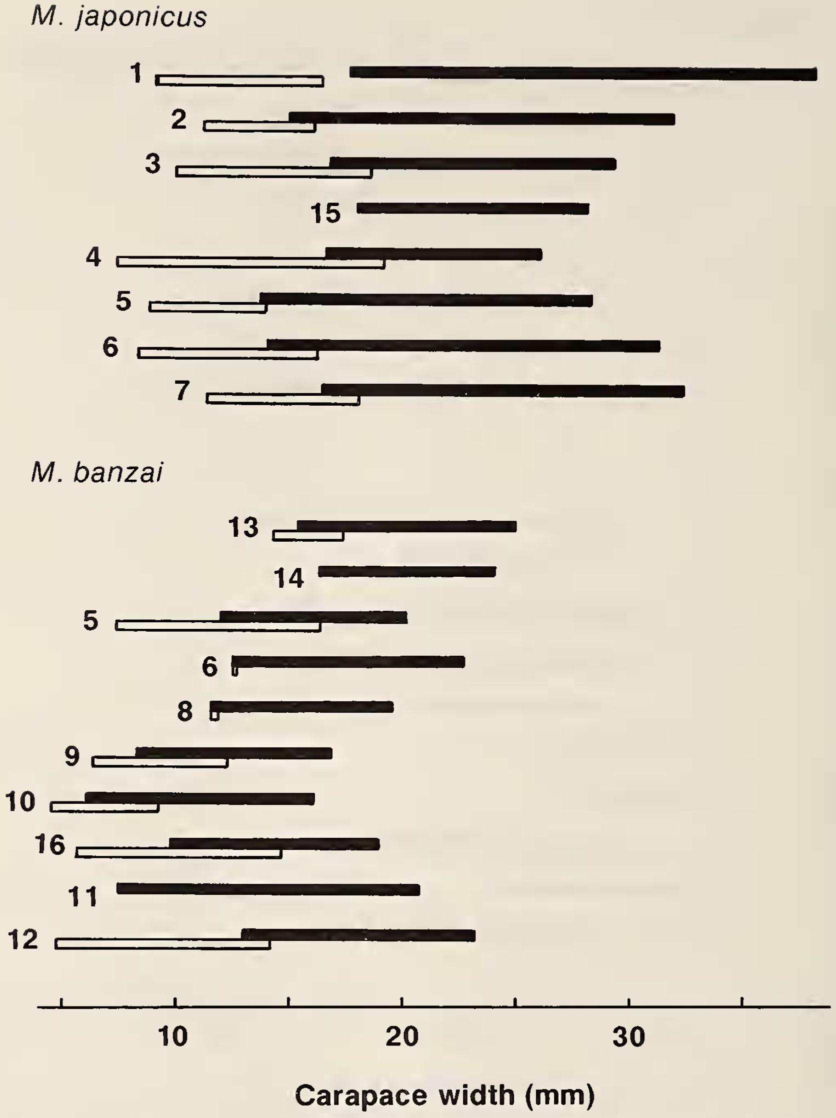

FIG. 4. Ranges of carapace widths of female crabs with widened abdomens (solid bar) and with unwidened abdomens (open bar) in *Macrophthalmus japonicus* and *M. banzai* from various localities. Details as in Fig. 3.

which showed larger sizes at puberty (Figs. 3 and 4), were slightly smaller than those of other populations.

DISCUSSION

According to the distributional records *Macrophthalmus japonicus* is distributed more northward than *M. banzai. M. japonicus* may be adapted to cool waters, whereas *M. banzai* to warm waters. The surface water current is probably most effective for dispersion of the two species. The dominant water current (the Kuroshio) in north-west Pacific region is inferred to have run northwards since the Eocene [6] when ocypodid crabs appeared as fossils [7]. The present distribution of the two species, therefore, would have been formed mainly by their northerly extension.

In closely related animal species, reproductive character displacement that prevent interbreeding

Table 4. Constants for regression equations (log Y=log a+b log X) (X: carapace width in mm; Y: propodus length of cheliped in mm) in fully-matured males of *Macrophthalmus japonicus* and *M. banzai* from various localities. For the criterion of fully-matured males, see the text. The localities (1–16) as in Fig. 1. They are arranged according to the latitude for each species. N: sample numbers

Locality	N	Range (X)	log a	b	r
M. japonicus					
1	35	23.55–39.95	−1.630	1.997	0.974
2	15	20.80–28.85	−2.660	2.787	0.955
3	12	27.05–33.45	−2.047	2.247	0.948
15	21	19.20–27.20	−2.382	2.623	0.902
4	12	21.00–27.80	−2.128	2.356	0.929
5	42	20.75–31.10	−1.719	2.105	0.913
6	24	18.30–30.30	−0.971	1.588	0.901
7	25	21.25–33.55	−2.002	2.284	0.962
M. banzai					
13	9	15.40–29.45	−1.273	1.809	0.982
14	19	15.05–23.70	−1.278	1.819	0.957
5	50	14.45–23.05	−1.052	1.727	0.939
6	34	14.10–26.30	−1.777	2.262	0.939
8	49	12.00–21.30	−1.727	2.270	0.966
9	33	11.00–15.90	−1.565	2.210	0.930
10	37	10.80–14.75	−0.975	1.743	0.897
16	25	16.25–24.70	−1.330	1.917	0.952
11	25	13.05–17.95	−1.295	1.986	0.871
12	50	16.25–25.10	−0.986	1.672	0.897

has been described for premating behaviors [8] or body coloration [9]. As with ocypodid crabs, Salmon *et al.* [10] demonstrated the existence of character displacement in acoustic signals of a premating behavior between two sibling species of *Uca pugilator* and *U. panacea,* but character displacement of waving display has not been reported. The pattern of waving display by *M. japonicus* and *M. banzai* did not differ within the same species among localities, irrespective of the co-occurrence with the opposite species. The wave duration of each species differed not only in localities, but also in periods at the same locality, and was assumed to be related to ambient temperatures at recording. Since *M. japonicus* and *M. banzai* differ remarkably in both the pattern of waving display [1] and behavioral sequence of pair formation [11], interbreeding is probably prevented in the overlap zone without exaggeration of difference in the pattern of waving display.

The Bergmann's rule is known to be occasionally applicable not only to endotherms but also to ectotherms including many invertebrates [12]. Among decapod crustaceans, for instance, the populations of the brachyurans *Cyclograpsus cinereus* [13], *Sesarma reticulatum* [14], *Helice crassa* [15] and *Pachygrapsus crassipes* [16] increase in body size according to the increase of the latitude, though there are some exceptions to this patten as seen in *Panopeus herbstii* and *Hemigrapsus oregonensis* [16]. The female of rock lobster *Jasus edwardsii* shows an inverse relationship between the size at the onset of sexual maturity and the water temperature of localities [17]. As with *M. japonicus* and *M. banzai,* the body sizes at puberty were larger in the former northern species than in the latter sourthern species, which is concordant with the Bergmann's rule.

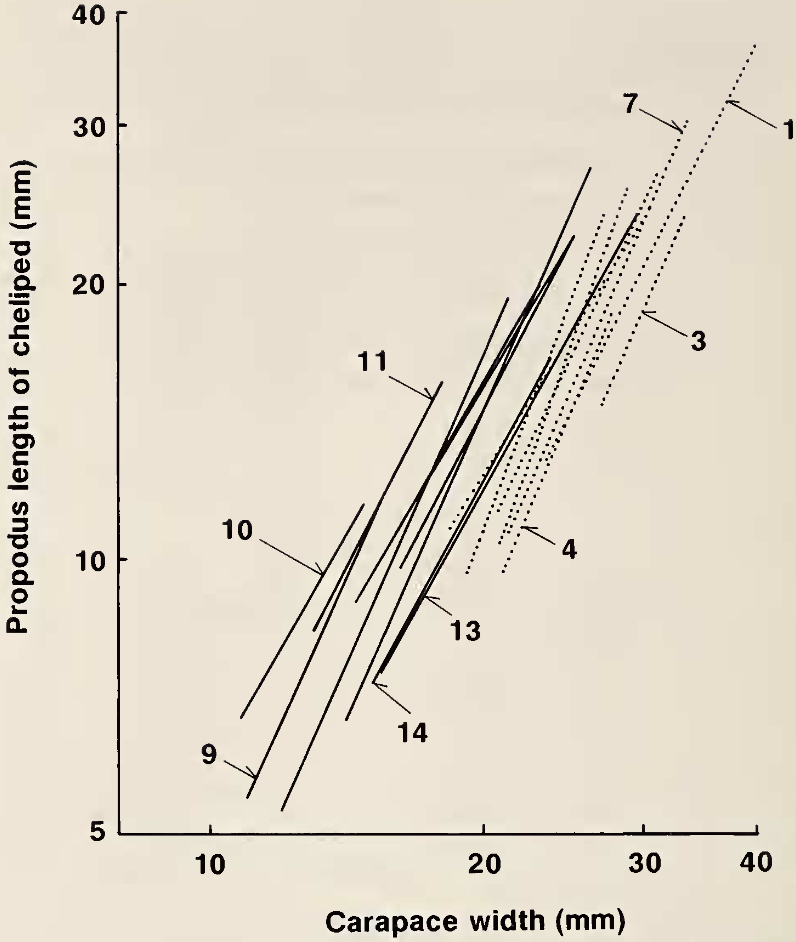

FIG. 5. Regression lines between carapace width and propodus length of cheliped of fully-matured males in *Macrophthalmus japonicus* (dotted line) and *M. banzai* (solid line) from various localities. Numerals by lines refer to the localities as in Fig. 1. As for the criterion of fully-matured males, see the text.

Among populations of each species, however, the size at puberty did not necessarily shows a clear trend following the Bergmann's rule. *M. japonicus* had larger puberty sizes in the populations occurring near the northern (Aomori Pref.) and southern (Kagoshima Pref.) limits of its range, and in the two intermediate localities (Chiba and Mie Prefs.). In *M. banzai* the two Korean populations occurring near the northern limit of its range had larger puberty sizes than other populations. But the sizes did not decrease according to the decrease of the latitude straightforwardly: the sizes were smaller in the populations from Amami-Ôshima, Okinawa-jima and Miyako-jima Isls., not only than in further northern populations but also than in further southern ones. In addition, relative proportions of CL, CW and PL in *M. banzai* revealed serial geographic variations concordant with puberty sizes: CL relative to CW in both sexes and CW relative to PL in fully-matured males were larger in the two Korean populations and smaller in the above three island populations than in others. Such a pattern observed in these morphometric characters of *M. banzai* seems to be related to the degree of oceanic to thalassic situation of localities, because the two Korean localities are situated at the innermost part of a large marginal sea of Yellow Sea and East China Sea, while the three Islands of Amami-Ôshima, Okinawa-jima and Miyako-jima Isls. are at the outermost part of it (see Fig. 1). The puberty size of *M. japonicus* also seems to be related to the similar conditions. Larger puberty sizes of the species were recorded from the localities situated in largely-sheltered bays (Locality Nos. 1, 3, 4, 7 in Fig. 1), while smaller puberty sizes from ocean-exposed ones (Locality Nos. 2, 5, 6 in Fig. 1). Similar phenomena have been reported as follows. The intertidal whelk *Nucella lapillus* matures at a smaller size at exposed shore than at protected one [18]. The body size at maturity of the grapsid crab *Hemigrapsus oregonensis* is larger in slough and lagoon population than in harbor one [16]. In the euryalid crab *Acanthocyclus albatrossis* CL relative to CW is largest in the most protected localities and smallest in the most exposed ones [13].

Although temperature is significant in the Bergmann's rule, the biogeographic patterns in body size and proportions observed in each of *M. japonicus* and *M. banzai* indicate importance of other environmental factors associated with oceanic to thalassic or exposed to sheltered gradients for geographic variation in morphology.

ACKNOWLEDGMENTS

I am grateful to Drs. B. L. Choe, H. Mukai, S. Saba and S. Takeda for their kind supplying specimens. Critical comments on the manuscript were provided by Drs. E. Harada, R. G. Hartnoll and two anonymous referees. Drs. M. Tsuchiya and M. Satô, and Messrs. C. H. Wang, M. Nishimura and M. Kiyota assisted me in field work. This work was supported in part by a Grant-in-Aid of Scientific Research (Nos. 56740320, 57740417) and Special Project Research (Nos. 58121001, 59115001, 60107001) from the Ministry of Education, Science and Culture of Japan.

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